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CHROMOSOME NUMBERS OF TREE SPECIES OF A LOWLAND TROPICAL COMMUNITY

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K. S. BAWA

CHROMOSOMAL CYTOLOGY HAS PLAYED a significant role in elucidating cytogenetic relationships among higher plants of the North Temperate Zone. However, for plants of the tropics, especially trees, even the chromosome numbers are not known for most species. Cytological data are particularly scarce for trees of the neotropics since almost all available data are from Asiatic or African species (see for example, Mangenot & Mangenot, 1962; Mehra & Bawa, 1969; Styles & Vosa, 1971; Hans, 1972). This paper reports chromosome numbers of tree species of a lowland tropical semideciduous forest in Costa Rica. A total of 66 species in 56 genera from 32 families were investigated; chromosome counts for 45 species and 16 genera were made for the first time.

MATERIAL AND METHODS

Material for chromosomal studies was collected from Hacienda Ciruelas, 5 km. northwest of Bagaces and Hacienda La Pacifica, 5 km. northwest of Cañas in Guanacaste Province, Costa Rica. The vegetation of these sites has been described in detail by Holdridge *et al.* (1971) and Daubenmire (1972), and need not be elaborated upon here. Floral buds were fixed in acetic alcohol (1:3), and after 24 to 28 hours transferred to 70 per cent alcohol. The buds were then stored at 0° C until the time of cytological examination. Standard cytological techniques (Sharma & Sharma, 1965) were employed for the study of chromosomes. In most species observations were made of material from two or three individuals.

Voucher specimens have been deposited in the Herbarium, Missouri Botanical Garden, St. Louis, Missouri, U.S.A. (MO).

RESULTS AND INTERPRETATION

The results are summarized in TABLE 1 in which are listed chromosome numbers together with ploidy level and previous cytological reports, if any, for all investigated taxa.

A detailed interpretation of chromosome numbers in each family must await accumulation of more data; however, numbers of a few taxa merit some comments which are presented below:

LEGUMINOSAE The present report of n = 11 for Andira inermis, and n = 10 for

BAWA, CHROMOSOME NUMBERS OF TREE SPECIES 1973] 423 Piscidia carthagenensis differs from n = 10 and n = 11 reported for those

species, respectively, by Atchison (1951).

MALPIGHIACEAE

The current finding of n = 12 for Byrsonima crassifolia from several different localities is at variance with 2n = 20 reported for this species by Nanda (1962). The same is true for Malpighia glabra in which the gametic number was observed to be n = 10 in contrast to 2n = 40 reported by Pal (1964).

Kyhos (1966) has found 2n = 12 in Galphimia glauca. It is, therefore, likely that x = 12, reported in several taxa of Malpighiaceae, is of polyploid derivation.

BOMBACACEAE

The family is characterized by the presence of high chromosome numbers. With the exception of Durio zibethinus (n = 28) all other taxa have n = 36 or more. The present report of n = 45 for Ochroma pyramidale differs from n = 36, 39, and 44 reported for this species under the name of O. lagopus by Baker and Baker (1968). In addition, Bombacopsis quinata was observed to have n = 46, but Baker and Baker (l.c.) recorded n = 36 for this species. The infraspecific variation in chromosome numbers also exists in several other taxa of the family. The variation in chromosome numbers could be, a) due to errors in the counting of chromosomes which could result from incomplete separation of a large number of chromosomes at metaphase or, b) due to the presence of accessory chromosomes. The first possibility is minimized by the fact that counts

by Baker and Baker and those reported here are based on observations of many cells from several individuals. The second possibility has been discussed by Baker and Baker, but the presence of accessory chromosomes remains to be established. The present data do not indicate the occurrence of accessory chromosomes because the same number of bivalents was observed in each cell. Clearly, more intensive cytological work on the family is needed to establish the true nature of chromosomal variability. The basic number in the family is probably x = 9, and the whole assemblage appears to be an ancient polyploid series.

BORAGINACEAE

The genus Cordia shows remarkable variation in chromosome numbers at the interspecific level; such variation is uncommon in tropical woody genera. According to Britton (1951), the base number of the genus is x = 8 because two species from India are reported to have 2n = 16. The present report of n = 15 for C. alliodora from several individuals contrasts sharply with 2n = 72 found by Britton (1951) in this species. I have no doubt about the correct identification of my voucher specimens, but I have been unable to check Britton's material. Since C. alliodora is a species of major importance to forestry in Central America, more intensive investigations are needed to detect the pattern of intraspecific variability in chromosome numbers, if it exists.

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DISCUSSION

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A common feature that most trees share is the high basic number: in 48 out of 56 genera the basic chromosome number is x = 11 or more. The same is true for tropical woody genera investigated from Africa and Asia (Mangenot & Mangenot, 1962, Mehra & Bawa, 1969). To the extent that the recombination index is a function of chromosome number, the high chromosome number must lead to an increase in the number of recombinants among the gametes of an individual (Lewis & John, 1963). The obligatory outcrossing mechanisms that characterize a majority of trees mentioned in this report (Bawa, 1973) further increase the number of recombinants but now among the zygotes. Thus both the meiotic system and the breeding system in tropical trees supplement each other in increasing the array of genotypes that result from a given reproductive cycle. It is beyond the scope of this paper to deal with the significance of the vast recombination potential of the genetic systems that appear to characterize most tropical trees investigated so far, but it needs to be emphasized that most tropical tree species are not characterized by the presence of a genetic system that conserves variation as is often assumed (see for example Catinot, 1972, Fedorov, 1966). It is not only the tropical woody genera that have high basic numbers; genera in some herbaceous families of the tropics such as Bromeliaceae, Commelinaceae, and Orchidaceae also have basic numbers that exceed x = 11 (cf. Stebbins, 1971). However, in those families that contain both herbaceous and woody taxa as, for example, the Leguminosae which are cytologically well known, the former have a lower basic number than the latter (Atchison, 1951; Solbrig, 1972). Grant (1963) has also pointed out a similar difference in the basic numbers of herbaceous and woody taxa of flowering plants in general. According to Ehrendorfer et al. (1968), the numbers higher than x = 11in woody angiosperms are probably of polyploid origin. If this assumption is correct, polyploids among the Costa Rican tree species amount to 70 per cent. However, if all chromosome numbers are considered as diploid unless they are multiples of lower numbers found in related genera, the frequency of polyploids is reduced to about 50 per cent. The true percentage of polyploids probably lies between these two extremes. Since one third to one half of all angiosperms are presumed to be polyploid (Hanelt, 1966; Löve & Löve, 1967; Grant, 1971; Stebbins, 1971; de Wet, 1971), the frequency of polyploidy among tropical trees is higher

than in flowering plants as a whole.

Although the frequency of polyploids among tropical woody taxa is high, polyploid series within genera are not common (Stebbins, 1971). As shown in TABLE II most genera found in the semideciduous forest have evolved at either the diploid or at the polyploid level: genera which contain diploid species have few or no polyploids and those which contain polyploid species have few or no diploids. Furthermore, in the latter NAME

FAGACEAE **Quercus oleoides Cham. & Schlecht.

ULMACEAE **Trema micrantha (L.) Blume

MORACEAE Cecropia peltata L.

PROTEACEAE

*Roupala complicata HBK.

OLACACEAE

*Ximenia americana L.

POLYGONACEAE

**Triplaris americana L.

ANNONACEAE

**Annona purpurea Moc. & Sessé
**A. reticulata L.
*Sapranthus palanga R. E. Fries

LAURACEAE **Ocotea veraguensis Mez

	1. Summary of Cytolog		
VOUCHER NUMBER	GAMETIC CHROMOSOME NUMBER	PLOIDY LEVEL	PREVIOUS REPORT
119	12	diploid	
252	10	diploid	
265	14	diploid	2n = 28: Krause, 1931
269	14	tetraploid	
169	13	?	
239	11	diploid	
247	7	diploid	
202 142	7 9	diploid diploid	
127	12	diploid	

TABLE I: Summary of cytological results.



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TABLE I: Summary of cytological results. (Continued)

NAME	Voucher Number	GAMETIC CHROMOSOME NUMBER	Ploidy Level	PREVIOUS REPORT
CAPPARACEAE				
**Crataeva tapia L.	240	13	2	
LEGUMINOSAE: Mimosoideae				
Enterolobium cyclocarpum (Jacq.) Griseb.	170	13	diploid	2n = 26: Atchison, 1951
**Pithecolobium racemiflorum Donn. Smith	270	13	diploid	
P. saman (Jacq.) Benth.	195	13	diploid	2n = 26: Atchison, 1951 Simmonds, 1954
LEGUMINOSAE: Caesalpinioideae				Simmonus, 1954
Cassia biflora L.	165	14	tetraploid	2n = 28: Irwin &
Hymenaea courbaril L.	168	12	diploid	Turner, 1960 2n = 24: Atchison, 1954; Berger <i>et al.</i> , 1958
LEGUMINOSAE: Papilionoideae				Derger et ut., 1950
Andira inermis (Swartz) HBK.	129	11	diploid	
**Dalbergia retusa Hemsl.	191	10	diploid	2n = 20: Atchison, 1951
**Lonchocarpus costaricensis (Donn. Smith) Pittier	184	11	diploid	
**L. eriocarinalis Micheli	100			
**L. guatemalensis Benth.	190	11	diploid	
**L. nitidus (Vog.) Benth.	261	11	diploid	
complex (vog.) Benth.	216	11	diploid	

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264	10	diploid	2n = 22: Atchison, 1951	
271	0			1
4/1	9	diploid		
125	10	diploid		
110	16	tetraploid		
268	12	diploid		
211	12	diploid		
	271 125 110 268	271 9 125 10 110 16 268 12	2719diploid12510diploid11016tetraploid26812diploid	10diploid $2n = 22$: Atchison, 1931 271 9diploid 125 10diploid 110 16tetraploid 268 12diploid

MELIACEAE

ABERS

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**Trichilia arborea C. DC.	272	25	tetraploid	
MALPIGHIACEAE				
Byrsonima crassifolia (L.) HBK.	118	12	tetraploid?	2n = 20: Nanda, 1962
Malpighia glabra L.	163	10	diploid?	2n = 24: Fouët, 1966 2n = 40: Pal, 1964
EUPHORBIACEAE				
*Bernardia nicaraguensis Standl. & L. O. Williams	177	26	tetraploid	
Garcia nutans Rohr	259	33	hexaploid	2n = 36: Miller & Webster,
Hura crepitans L.	221	22	tetraploid	1966 2n = 36: Miège, 1962
				2n = 44: Datta, 1967
ANACARDIACEAE				
Spondias mombin L.	183	16	tetraploid	2n = 32: Simmonds, 1954

NAME	Voucher Number	GAMETIC CHROMOSOME NUMBER	Ploidy Level	PREVIOUS REPORT
HIPPOCRATEACEAE				
*Hemiangium excelsum (HBK.) A. C. Smith	156	30	tetraploid	
SAPINDACEAE				
*Allophylus occidentalis (Swartz) Radlk.	210	14	tetraploid	
*Cupania americana L.	108	16	tetraploid	
*Thouinidium decandrum (Humb. & Bonpl.) Radlk.	133	ca. 14	tetraploid	
ELAEOCARPACEAE				
*Muntingia calabura L.	120	14	tetraploid	
*Sloanea terniflora (Moc. & Sessé) Standl.	149	13	tetraploid	
TILIACEAE				
*Apeiba tibourbou Aubl.	205	18	tetraploid	
Luehea candida (Moc. & Sessé) Mart. & Zucc	198	18	tetraploid	2n = 36: Gadella <i>et al.</i> , 1969
BOMBACACEAE				
Bombacopsis quinata (Jacq.) Dugand	106	46	decaploid?	2n = 72: Baker & Baker, 1968
Ochroma pyramidale (Cav. ex Lam.) Urban	145	45	decaploid?	2n = 72, 78, 88: Baker & Baker, 1968

**Pseudobombax septenatum (Jacq.) Dugand	141	ca. 44	decaploid?	
STERCULIACEAE Guazuma tomentosa HBK. **Sterculia apetala (Jacq.) Karst.	132 187	8 20	diploid tetraploid	2n = 16: Youngman, 1931
DILLENIACEAE *Curatella americana L.	116	ca. 12	diploid	
OCHNACEAE **Ouratea wrightii Riley	185	13	diploid	
MYRSINACEAE **Ardisia revoluta HBK.	162	23	tetraploid	
THEOPHRASTACEAE Jacquinia aurantiaca Ait.	111	18	tetraploid	2n = 36: Faure, 1968
SAPOTACEAE **Manilkara zapota (L.)	214	12	diploid	
P. van Royen *Mastichodendron capiri Cronquist var. tempisque (Pittier) Cronquist	146	11	diploid	
EBENACEAE **Diospyros nicaraguensis Standl.	204	15	diploid	
Styracaceae **Styrax argenteus Presl	114	8	diploid	

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NUMBERS OF -REE SPECIES

NAME

APOCYNACEAE Plumeria rubra L. var. acutifolia Poir.

> *Stemmadenia donnell-smithii (Rose) Woodson

BORAGINACEAE

*Bourreria quirosii Standl. Cordia alliodora (Ruiz & Pav.) Cham.

**C. collococca Sond.

**C. dentata Poir.

**C. panamensis Riley

**C. inerma (Mill.) Johnston

BIGNONIACEAE

Tabebuia rosea (Bertol.) DC.

T. palmeri Rose

* Genera investigated for the first time. ** Species investigated for the first time.

Voucher Number	GAMETIC CHROMOSOME NUMBER	PLOIDY LEVEL	PREVIOUS REPORT
167	18	tetraploid	2n = 36: Singh, 1954; Tapadar & S Nanda, 1962
176	19	tetraploid	
148	19	2	
105	15	tetraploid	2n = 72: Britton, 195
199	14	tetraploid	
229	24	hexaploid	
217	14	tetraploid	
223	14	tetraploid	
126	20	diploid	2n = 40: Venkatasubl
273	20	diploid	2n = 40: Pathak et al

TABLE I: Summary of cytological results

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TABLE II: Frequency of polyploid species in woody genera of a lowland tropical semideciduous forest in Costa Rica.1,2

NAME	BASIC NUMBER	NUMBER OF DIPLOID SPECIES	NUMBER OF POLYPLOID SPECIES
Piper	13	7	6
Piper Annona	7	7	2
Bauhinia	7		15
Cassia	7	31	84
Caesalpinia	12	20	
Acacia	13	66	27
Albizia	13	13	2
Pithecolobium	13	8	1
Lonchocarpus	11	13	1
Pterocarpus	11	7	2
Zanthoxylum	9?		. 6
Trichilia	14	1	8
Cedrela	12?		8
Malpighia	10	4	1
Margaritaria	7	2	19
Sterculia	10		9
Ouratea	12	12	1
Eugenia	11	8	7
Ardisia		1	6
Diospyros	15	13	6
Plumeria	9		5
Cordia	8		15
Tabebuia	20	10	
Psychotria	11	16	2

L 11	ychochoc	11	10	122

¹ Based on chromosome counts reported in Bolkhovskikh et al. (1969).

² Only those genera in which chromosome counts for more than five species are known are tabulated.

group of genera, within a genus most species usually have the same ploidy level.

Polyploid series within species are also not common, but rarely have tropical tree species been subjected to the sort of intensive studies that are necessary to reveal intraspecific variability in chromosome numbers; in most species investigated to date, chromosome counts have been based on the study of few individuals. Among species mentioned in this report, Cordia alliodora, Ochroma pyramidale, Bombacopsis quinata and Pseudobombax septenatum appear to have polyploid series (TABLE I). The reasons for the low frequency of polyploid series have been pointed out by Stebbins (1971), and need not be elaborated upon here.

SUMMARY

This paper reports chromosome numbers of tree species of a lowland tropical semideciduous forest in Costa Rica. A total of 66 species in

56 genera from 32 families were investigated, chromosome counts for 45 species and 16 genera were made for the first time. A common feature of most species is the high basic number; in 48 out of 56 genera, the basic number is x = 11 or more. Such numbers are probably of polyploid derivation. However, although the frequency of polyploids among tropical woody taxa is high, polyploid series within genera and species are rare.

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LITERATURE CITED

ATCHISON, E. 1951. Studies in the Leguminosae VI. Chromosome numbers among tropical woody species. Am. Jour. Bot. 38: 538-546.
BAKER, H. G., & I. BAKER. 1968. Chromosome numbers in the Bombacaceae. Bot. Gaz. 129: 294-296.

- BAWA, K. S. 1973. Breeding systems of tree species of a lowland tropical community. Evolution (in press).
- BERGER, C. A., E. R. WITKUS, & R. M. MCMAHON. 1958. Cytotaxonomic studies in the Leguminosae. Bull. Torrey Bot. Club. 85: 405-414.
- BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. 1969. Chromosome numbers of flowering plants. Komarov Botanical Institute, Leningrad. 996 pp.
- BORGMANN, E. 1964. Anteil der Polyploiden in der Flora des Bismarcksgebirges von Ostneuguinea. Bot. Zeitschr. 52: 118-173.
- BRITTON, D. M. 1951. Cytogenetic studies on the Boraginaceae. Brittonia 7: 233-266.
- CATINOT, R. 1972. Biological and economic opportunities and limitations to the manipulations of the tropical forest ecosystem. Proc. Seventh World Forestry Congress. Buenos Aires, Argentina (in press).
- DATTA, N. 1967. In IOPB chromosome number reports XII. Taxon 16: 344-349.
- DAUBENMIRE, R. 1972. Phenology and other characteristics of tropical semi-

deciduous forest in northwestern Costa Rica. Jour. Ecol. 60: 147-170.
DESAI, S. 1960. Cytology of Rutaceae and Simarubaceae. Cytologia 25: 28-35.
EHRENDORFER, F., F. KRENDEL, E. HABLER, & W. SAUER. 1968. Chromosome numbers and evolution in primitive angiosperms. Taxon 17: 337-353.
FAURE, P. 1968. Contribution a l'étude caryo-taxinomique des Myrsinaceae et des Theophrastaceae. Mém. Mus. Nat. Hist. Naturelle, Ser. B. 18: 37-58.

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- FEDOROV, A. A. 1966. The structure of tropical rain forest and speciation in the humid tropics. Jour. Ecol. 54: 1-11.
- Fouër, M. 1966. Contribution à l'étude cyto-taxonomique des Malpighiacées. Adansonia 6: 457-505.
- GADELLA, T. W. J., E. KLIPHUIS, J. LINDEMAN, & E. A. MENNEGA. 1969. Chromosome numbers and seedling morphology of some Angiospermae collected in Brazil. Acta. Bot. Neerl. 18: 74-83.
- GRANT, V. 1963. Origin of adaptations. Columbia Univ. Press, New York. 606 pp.

——. 1971. Plant speciation. Columbia Univ. Press, New York. 435 pp. HANELT, V. P. 1966. Polyploidie — Frequenz und geographische Verbreitung bei höheren Pflanzen. Biol. Rundschau 4: 185–196.

- HANS, A. S. 1972. Cytomorphology of arborescent Moraceae. Jour. Arnold Arb. 53: 216-225.
- HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHEWAY, T. LIANG, & J. A. TOSI, JR. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, New York. 747 pp.
- IRWIN, H. S., & B. L. TURNER. 1960. Chromosomal relationships and taxonomic considerations on the genus Cassia. Am. Jour. Bot. 47: 309-318.
- KRAUSE, O. 1931. Zytologische Studien bei den Urticales unter besonderer Berücksichtigung der Gattung Dorstenia. Planta 13: 29-84.
- Куноs, D. W. 1966. In: Documented chromosome numbers of plants. Madroño 18: 245, 246.
- LEWIS, K., & B. JOHN. 1963. Chromosome marker. Little, Brown & Co., Boston. 489 pp.
- LÖVE, A., & D. LÖVE. 1967. Polyploidy and altitude: Mt. Washington. Biol. Zentralblatt 86 (supplement): 307-322.
- MANGENOT, S., & G. MANGENOT. 1962. Enquète sur les nombres chromosomiques dans une collection d'espèces tropicales. Rév. Cytol. et Biol. Vég. 25: 411-447.
- MEHRA, P. N., & K. S. BAWA. 1969. Chromosomal evolution in tropical hardwoods. Evolution 23: 466-481.
- Miège, J. 1962. Quatrième liste de nombres chromosomiques d'espèces d'Afrique Occidentale. Rév. Cytol. et Biol. Vég. 24: 149-164.
- MILLER, K. I., & G. L. WEBSTER. 1966. Chromosome numbers in the Euphorbiaceae. Brittonia 18: 372-379.
- NANDA, P. C. 1962. Chromosome numbers of some trees and shrubs. Jour. Indian Bot. Soc. 4: 271-277.
- PAL, M. 1964. Chromosome numbers in some Indian angiosperms I. Proc. Indian Acad. Sci. 60: 347-350.
- РАТНАК, G. N., B. SINGH, K. M. TIWARI, A. N. SRIVASTAVA, & K. K. PANDE. 1949. Chromosome numbers in some angiospermous plants. Curr. Sci. 18: 347.
- SHARMA, A. K., & A. SHARMA. 1965. Chromosome techniques: theory and

practice. Butterworths, London. 474 pp.
SIMMONDS, N. W. 1954. Chromosome behaviour of some tropical plants. Heredity 8: 139-146.
SINGH, B. 1951. Chromosome numbers in some flowering plants. Curr. Sci. 20: 105.
SOLBRIG, O. T. 1972. Cytology and cytogenetics of shrubs. pp. 123-137. In: MCKELL, C. M., J. M. BLAISDELL, & J. R. GOODIN (Eds.). Wildland Shrubs

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- their biology and utilization. Intermountain Forest and Range Experiment Station, U.S. Dept. Agric. Ogden, Utah.

STEBBINS, G. L., JR. 1971. Chromosomal evolution in higher plants. Addison-Wesley, Reading, Massachusetts. 216 pp.

STYLES, B. T., & C. G. Vosa. 1971. Chromosome numbers in the Meliaceae. Taxon 20: 485-499.

 TAPADAR, N. N. R., & N. K. SEN. 1960. Cytotaxonomical studies on the economic plants of the family Apocynaceae. Caryologia 12: 367-397.
 VENKATASUBBAN, K. R. 1944. Cytological studies in Bignoniaceae. Annamali

Univ. Publ. 1, 2, and 3: 1-207.

WET, J. M. J. DE. 1971. Polyploidy and evolution in plants. Taxon 20: 29-35.
YOUNGMAN, W. 1931. Studies on the cytology of Hibisceae II. The behaviour of the nucleus during cell division in the root-tip of *Thespesia populnea* and comparative observations of the phenomenon in related plants. Ann. Bot. 45: 49-72.

GRAY HERBARIUM HARVARD UNIVERSITY CAMBRIDGE, MASSACHUSETTS 02138